

# Cumulative or sequential assessment during hermit crab shell fights: effects of oxygen on decision rules

Mark Briffa\* and Robert W. Elwood

*School of Biology and Biochemistry, The Queen's University of Belfast, 97 Lisburn Road, Belfast BT9 7BL, UK*

Agonistic interactions between animals are often settled by the use of repeated signals which advertise the resource-holding potential of the sender. According to the sequential assessment game this repetition increases the accuracy with which receivers may assess the signal, but under the cumulative assessment model the repeated performances accumulate to give a signal of stamina. These models may be distinguished by the temporal pattern of signalling they predict and by the decision rules used by the contestants. Hermit crabs engage in shell fights over possession of the gastropod shells that they inhabit. During these interactions the two roles of signaller and receiver may be examined separately because they are fixed for the duration of the encounter. Attackers rap their shell against that of the defender in a series of bouts whereas defenders remain tightly withdrawn into their shells for the duration of the contest. At the end of a fight the attacker may evict the defender from its shell or decide to give up without first effecting an eviction; the decision for defenders is either to maintain a grip on its shell or to release the shell and allow itself to be evicted. We manipulated fatigue levels separately for attackers and defenders, by varying the oxygen concentration of the water that they are held in prior to fighting, and examined the effects that this has on the likelihood of each decision and on the temporal pattern of rapping. We show that the vigour of rapping and the likelihood of eviction are reduced when the attacker is subjected to low oxygen but that this treatment has no effect on rates of eviction when applied to defenders. We conclude that defenders compare the vigour of rapping with an absolute threshold rather than with a relative threshold when making their decision. The data are compatible with the cumulative assessment model and with the idea that shell rapping signals the stamina of attackers, but do not fit the predictions of the sequential assessment game.

**Keywords:** aggression; signalling; hermit crab; assessment; stamina; evolutionarily stable strategy

## 1. INTRODUCTION

Agonistic encounters between animals are often resolved by the use of displays and signals, which advertise fighting ability or 'resource-holding potential' (RHP), rather than by direct fighting. By adopting the roles of signaller and receiver both participants reduce the risk of injury but incur energetic costs and time-costs. The signals used to advertise RHP are often performed repeatedly and organized into a series of bouts. Repeated signalling would be more costly than a single performance and there are various game theoretical models that assume different reasons for repetition. The sequential assessment model (Enquist & Leimar 1983; Enquist *et al.* 1990), for example, suggests that repeated performances enable receivers to make an accurate assessment of the factor being advertised. An alternative way in which signallers could advertise their RHP is to repeatedly perform a demanding activity such that the performances accumulate to give a measure of their quality. The ability to perform the signal might then be determined by the individual's stamina. Under the energetic war of attrition (Payne & Pagel 1996, 1997) and the cumulative assessment model (Payne 1998) any such measure would be given by a combination of the rate of performance and the duration of the contest, and would represent the total energy expenditure of the signaller. Thus, the rate and duration of activity and likelihood of victory might be mediated by fatigue.

These models may be distinguished by the decision rules used by the contestants. In the sequential assessment model (Enquist & Leimar 1983, 1987; Enquist *et al.* 1990) the receiver's assessment of its opponent's fighting ability, at any given point in the contest, represents the average difference between its own fighting ability and the estimated fighting ability of the opponent. Thus, receivers assess their opponent's relative fighting ability and the accuracy of this assessment is predicted to increase as the contest progresses. The evolutionarily stable strategy (ESS) for this model is to use a threshold level of the opponent's relative fighting ability as a 'switching line' such that when the estimate of the opponent's RHP crosses this line the receiver gives up. Thus, receivers are expected to reach their decision by comparing the opponent's level of signalling with a relative threshold.

According to the energetic war of attrition (Payne & Pagel 1996, 1997) a contestant is expected to give up when the cumulative of its own displays crosses a threshold level. Under the cumulative assessment model, however, each contestant assesses the sum of its opponent's displays and is predicted to give up when the cumulative energy expenditure of the opponent crosses an absolute threshold (Payne 1998). Whereas the sequential assessment model predicts signals should be performed with constant intensity and wars of attrition predict that contestants should match the opponent's level of signalling, the cumulative assessment model allows both variation in the level of signalling during the course of the encounter and different levels of signalling between the contestants.

\*Author for correspondence (m.briffa@qub.ac.uk).

In practice, it is often difficult to examine the decision rules used by receivers or senders in isolation because an individual may alternate between the two roles during the course of an encounter. During 'roaring contests' between male red deer, *Cervus elaphus*, over access to females, for example, the contestants take turns at performing bouts of vocalizations and these interactions have been called 'conversations' (Clutton Brock *et al.* 1979; Clutton Brock & Albon 1979), and in birds, both contestants may sing in territorial disputes over perching sites (Lambrechts & Dhondt 1988; Weary *et al.* 1991). During 'shell fighting' in hermit crabs, however, the two roles remain fixed throughout the encounter such that receivers and signalers can be manipulated independently. These encounters are usually initiated by the larger of two crabs, which attacks the small crab in an attempt to gain possession of its shell. The large 'attacker' approaches the small 'defender' and both crabs display using their chelipeds. If the large crab decides to continue with the encounter it grasps the defender's shell between its walking legs and the defender withdraws tightly into its shell and remains in this position until the encounter is resolved. The attacker performs further investigatory activities on the defender's shell before beginning the key agonistic activity of shell rapping. It brings its own shell rapidly and repeatedly into contact with the shell of the defender in a series of bouts that are separated by pauses. After a number of bouts of rapping the attacker may pull the defender from its shell. In this case the attacker may move into the now available shell and the small crab may occupy the shell discarded by the attacker (Dowds & Elwood 1983, 1985; Elwood & Glass 1981; Elwood *et al.* 1998). An alternative explanation of shell exchange is that it results from a process of negotiation (Hazlett 1978, 1983, 1987, 1996). According to the negotiation model rapping allows the defending crab to assess the quality of the attacker's shell, perhaps by assessing the fundamental frequency of the rapping sound, which should be related to the volume of the shell. The defender would only allow an exchange to take place when this would lead to an increase in the quality of its shell.

Previous analysis of the temporal pattern of shell rapping demonstrates both escalation and de-escalation in vigour as predicted by the energetic war of attrition model (Payne & Pagel 1997), and shows that attackers that evict the opponent rap with greater vigour than those that are unsuccessful (Briffa *et al.* 1998). Furthermore, analysis of the within-bout structure of rapping shows that vigour decreases both within individual bouts and from bout to bout (Briffa & Elwood 2000a) suggesting that vigour could be determined by the level of fatigue. A cause of fatigue might be the accumulation of lactic acid in the blood, which has been shown to place a severe restriction on activity rates in crustaceans (Smith & Taylor 1993; Thorpe *et al.* 1995), and this could be caused by insufficient oxygen in the haemolymph. Thus we can experimentally vary the speed with which fatigue should occur by varying the concentration of oxygen in the water. Crabs exposed to low levels of oxygen concentration should become fatigued more rapidly than those exposed to high oxygen concentrations. Thus, if the vigour of rapping is determined by stamina, crabs treated with reduced oxygen levels should rap less vigorously and be less likely to effect an exchange.

It is unlikely that the only function of rapping is to signal the stamina of attackers and various detrimental effects for defenders, which reduce their ability to maintain an adequate grip on the shell, have been suggested. These include direct action on the abdominal muscles (Briffa & Elwood 2000b), disruption of the sensory organs (Elwood & Neil 1992) and disruption of the respiratory current of water causing an oxygen debt to accumulate (Elwood & Neil 1992). If rapping prevents defenders from respiring aerobically the accumulation of lactic acid may also influence their decision to give up. In this case it is predicted that the likelihood of an eviction and the speed with which an eviction may be effected would then be increased if defenders were exposed to conditions of low oxygen concentration.

## 2. MATERIAL AND METHODS

We collected littoral specimens from rock pools at Ballywalter, County Down, Northern Ireland, UK between July and October 1999. They were kept in the laboratory in groups of 75–100 in plastic tanks (60 cm × 30 cm), which were filled with aerated seawater to a depth of 10 cm, and fed twice weekly on catfish pellets. Crabs were used within one week and then returned to the sea.

We removed the crabs from their shells by cracking the shell in a bench vice and they were sexed using a binocular microscope. We only used male crabs that were free from (i) obvious parasites, (ii) missing appendages, and (iii) recent moult, because females show marked differences in shell preference during the breeding season. We provided females and unused males with new shells and returned them to the rock pools from which they were collected. We allocated the crabs to pairs consisting of a small and a large crab (mean weights  $\pm$  s.e.; small,  $0.187 \pm 0.005$  g; large,  $0.286 \pm 0.006$  g). We determined the preferred size of *Littorina obtusata* shell of each crab using regression lines that relate crab weight to preferred shell weight (obtained from shell selection experiments; Jackson 1988). We provided the small crab of each pair with an *L. obtusata* shell of the preferred weight of the large crab that it was paired with, whereas the large crab of each pair was provided with a shell that was 25% of its preferred weight, i.e. much too small.

We pre-treated crabs with oxyc (100% O<sub>2</sub> saturated  $\pm$  5% at 10 °C) or hypoxic (30% O<sub>2</sub> saturated  $\pm$  5% at 10 °C) seawater for 30 min prior to fights. We chose 30% O<sub>2</sub> saturation for the hypoxic treatment because this is the lower limit of oxygen concentration that hermit crabs are likely to experience in rock pools (Côté *et al.* 1998) and a pilot study demonstrated that fights were still initiated under these conditions. They were transferred from the crystallizing dishes into isolated plastic containers with sealable lids, containing 1 cm layer of clean sand and seawater. We adjusted the oxygen content of the seawater by bubbling with either nitrogen or oxygen through an air stone and we used a Jenway 9071 DO<sub>2</sub> meter (Jenway Ltd, Felsted, UK) to measure the per cent saturation.

It has been demonstrated that shell weight preferences alter under prolonged exposure to hypoxic conditions with crabs selecting shells over 50% lighter than normal after being held in hypoxic water for 24 h (Côté *et al.* 1998). In order to determine whether a 30 min pre-treatment with hypoxic water would alter subsequent shell preferences in oxyc water, we conducted a second pilot study where crabs were removed from their shells, weighed (mean weight  $\pm$  s.e. =  $0.28 \pm 0.01$  g) and isolated in

Table 1. *Number of observations with percentage of fights and exchanges of shells*

(In group OH large crabs (attackers) were pre-treated with oxalic water and small crabs (defenders) with hypoxic water; in group HO this was reversed; in group HH both crabs were pre-treated with hypoxic water and in group OO both were pre-treated with oxalic water. All tests quoted in the text were performed on raw data.)

group	observations ( <i>n</i> )	fights ( <i>n</i> )	exchanges ( <i>n</i> )	no exchanges ( <i>n</i> )	observations with fights (%)	fights with exchanges (%)
OH	38	16	11	5	42	69
HO	38	19	10	9	50	53
HH	38	13	7	6	34	54
OO	38	28	23	5	74	82
total	152	76	51	25	—	—

either oxalic ( $n = 20$ ) or hypoxic ( $n = 22$ ) water for 30 min before being transferred to a test arena consisting of a 95 mm crystallizing dish containing oxalic (100%  $O_2$  saturated  $\pm 5\%$  at  $10^\circ C$ ) water, a 1 cm layer of cleaned sand and ten *L. obtusata* shells ranging from 50 to 125% of the crab's preferred shell weight. The weights of the first shell and the shells occupied at 30 min, 1 h and 12 h were recorded. A one-factor ANCOVA with one repeated measure was performed in order to determine the effects of (i) the pre-treatment, (ii) time (repeated measure), and (iii) the weight of the crab (covariate) on the size of shell that was occupied. There was no difference in preferred shell weight between the two pre-treatments or between the different times, but the weight of shell occupied increased with crab weight ( $F_{1,38} = 136.4, p < 0.0001$ ).

We staged fights between four groups of paired crabs. In one group the large crabs were pre-treated as above with oxalic water and small crabs with hypoxic water; in a second this was reversed; in the third both crabs were pre-treated with hypoxic water and in a fourth both crabs were pre-treated with oxalic water. We isolated the crabs in 9 cm diameter crystallizing dishes filled with aerated seawater for ca. 18 h before applying the 30 min pre-treatments. We then transferred the two crabs to an oxygenated arena, containing 100%  $O_2$  saturated  $\pm 5\%$  water at  $10^\circ C$  as above, that was placed behind the one-way mirror of an observation chamber such that the observer could view the crabs but could not be seen by them. All fights in the present study were initiated by the larger of the two crabs. To measure the fine-scale timing of shell rapping, we used an Ultravox<sup>TM</sup> (Noldus Information Technology BV, Wageningen, The Netherlands) sound analysis system. The sound produced by the raps was fed into the Ultravox equipment via an ultrasound detector (QMC model SI00; Ultrasound Advice, London, UK). With the frequency set to broad band, the sensitive microphone of the ultrasound detector was able to register the 'audible' (to human hearing) frequencies of the individual raps. The Ultravox system allowed the timing of the rapping to be measured to the nearest 30 ms. Thus records of every rap in the encounter and the intervals between the raps were made. Gaps within bouts were typically less than 150 ms duration ( $\bar{X} \pm s.e. = 148.4 \pm 4.7$  ms) whereas the pause between bouts was typically greater than 13 s ( $\bar{X} \pm s.e. = 13.534.21 \pm 561.7$  ms), so we treated any gap  $< 1$  s between two consecutive raps as a pause between two consecutive bouts. We also kept a written record of the outcome of the encounters.

### 3. RESULTS

A total of 152 observations were made that produced 76 fights, 51 of which resulted in an exchange. There was

a strong non-significant trend for large crabs treated with oxalic water to initiate more fights than those in the hypoxic water groups ( $G_1 = 3.8, p = 0.055$ ) (table 1) and attackers treated with oxalic water that initiated fights were more likely to effect an exchange than those that were treated with hypoxic water ( $G_1 = 4.88, p < 0.05$ ). Small crabs that were treated with oxalic water were more likely to be attacked than those treated with hypoxic water ( $G_1 = 8.6, p < 0.005$ ) but there was no difference in the likelihood of defenders being evicted between those treated with oxalic water and those treated with hypoxic water. We calculated relative weight difference (RWD) between the pairs of crabs as  $1 - (\text{weight of small crab} / \text{weight of large crab})$ . There was no difference in RWD between the groups of staged fights or between the groups for fights that were initiated.

Three-factor ANCOVAs with two repeated measures were used to examine variation in the duration of gaps. The three factors were (i) the pre-treatment applied to initiators, (ii) the pre-treatment applied to defenders, and (iii) the outcome of the encounter and the regressor was the RWD between the two crabs. The two repeated measures were the position of the bout within the fight and the position of the gap within the bout. The mean number of bouts in a fight  $\pm s.e.$  was  $16.42 \pm 2.3$  and the durations of the first and last four gaps of the first six bouts were examined. This allowed us to include the majority of fights in the analysis (14 fights were excluded because they contained less than six bouts of rapping). We used separate ANCOVAs for the first and last four gaps because the bouts were of variable length. To minimize overlap in the data used for the two analyses, we used only bouts containing at least eight raps for the second analysis whereas the first contained all bouts that had at least five raps. Thus the degrees of freedom vary between the two analyses. Two additional repeated-measures four-factor ANCOVAs were performed to determine how (i) the duration of the intervals between the first six bouts ('pauses'), and (ii) the number of raps contained in each of the first six bouts varied as the fight progressed.

#### (a) *The first four gaps in each bout*

In the first part of each bout, attackers that were pre-treated with oxalic water left shorter gaps between raps than did those pre-treated with hypoxic water ( $F_{1,34} = 14.4, p < 0.001$ ) (figure 1a) but the duration of the gaps was not influenced by the pre-treatment applied to defenders, RWD or the outcome of the encounter. There

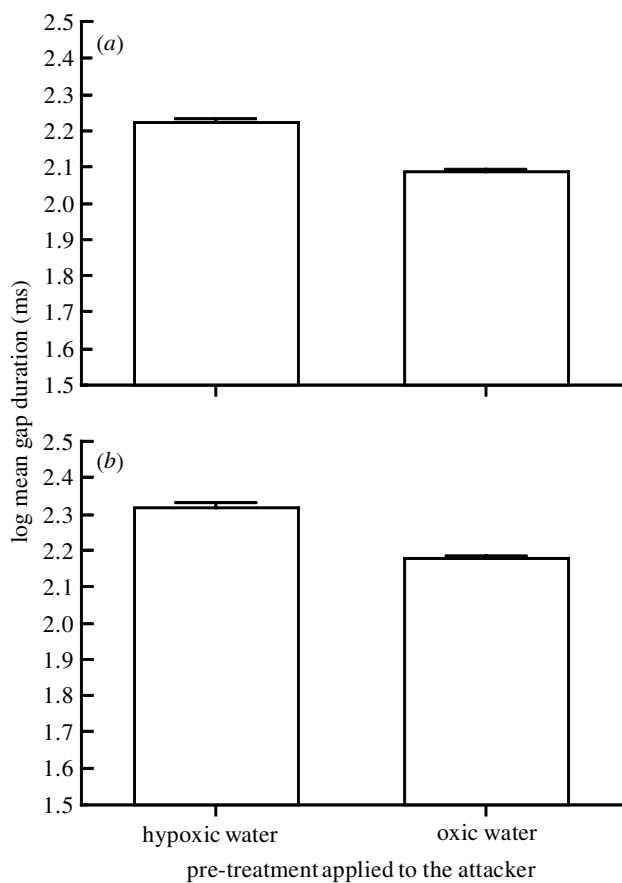


Figure 1. The effect of the pre-treatment applied to the attacker on the mean duration of (a) the first four gaps and (b) the last four gaps of the first six bouts of rapping. Error bars show s.e.

was a two-factor interaction between the pre-treatment of attackers and that of defenders ( $F_{1,34} = 7.8, p < 0.01$ ) (figure 2a); when the defender was given the hypoxic treatment the treatment of the attacker had little effect on the gaps but when the defender was given oxic treatment attackers also given the oxic treatment had shorter gaps than those given hypoxic treatment. There was also a two-factor interaction between the outcome of the encounter and the pre-treatment of the defender ( $F_{1,34} = 4.7, p < 0.05$ ) (figure 3a); crabs that effected an exchange with hypoxic defenders left longer gaps between raps than with oxic defenders but when there was no exchange there was no difference in gap duration between the two treatments applied to defenders.

Overall, the duration of the gaps did not change from bout to bout. There was, however, a significant interaction between bout number and the pre-treatment of the attacker ( $F_{5,170} = 3.0, p < 0.01$ ) (figure 4), with the duration of the gaps increasing from bout to bout in crabs pre-treated with oxic water and the gap durations being consistently higher for crabs pre-treated with hypoxic water. There were no further interaction effects. The durations of the gaps also varied within bouts ( $F_{3,102} = 7.9, p < 0.0001$ ). Comparisons of means show that the duration of gap 1 is greater than that of gap 2 ( $F_{1,102} = 12.6, p < 0.001$ ), the duration of gap 2 is less than that of gap 3 ( $F_{1,102} = 33.7, p < 0.0001$ ) and the duration of gap 3 is less than that of gap 4 ( $F_{1,102} = 4.1, p < 0.05$ ). There were no interaction effects.

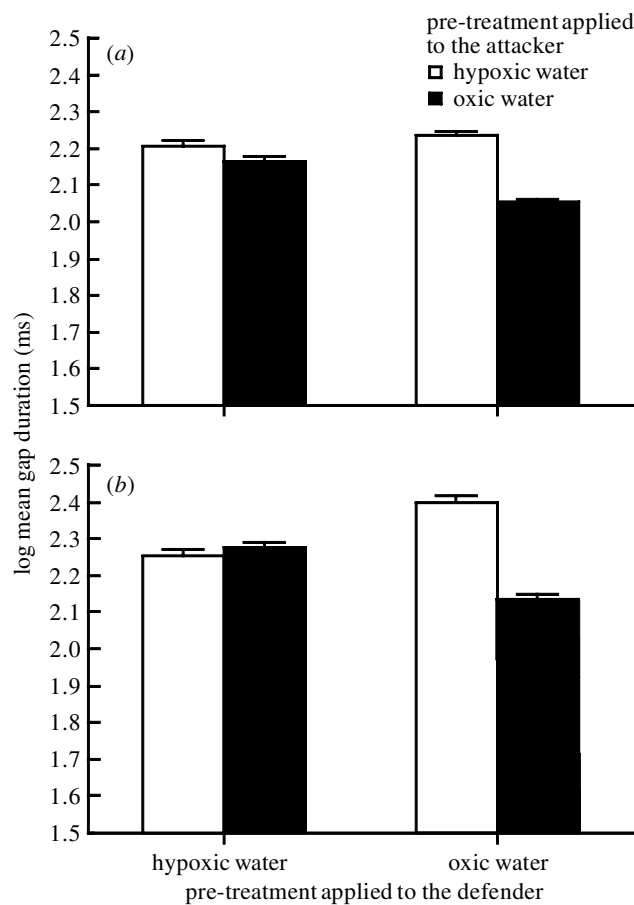


Figure 2. The interaction effect between pre-treatments applied to attackers and defenders on the duration of (a) the first four gaps and (b) the last four gaps of the first six bouts of rapping. Error bars show s.e.

(b) *The last four gaps in each bout*

In the last phase of each bout attackers that were pre-treated with oxic water left shorter gaps between raps than did those pre-treated with hypoxic water ( $F_{1,25} = 7.6, p < 0.01$ ) (figure 1b), but the duration was not influenced by the pre-treatment applied to defenders, the outcome of the encounter or RWD. There was a two-factor interaction between the pre-treatment of attackers and that of defenders ( $F_{1,25} = 9.8, p < 0.005$ ) (figure 2b); when the defender was given the hypoxic treatment the treatment of the attacker had little effect on the gaps but when the defender was given oxic treatment, attackers also given the oxic treatment had shorter gaps than those given hypoxic treatment. There was also a two-factor interaction between the outcome of the encounter and the pre-treatment of the defender ( $F_{1,25} = 4.5, p < 0.05$ ) (figure 3b); crabs that effected an exchange with hypoxic defenders left longer gaps between raps than with oxic defenders but when there was no exchange there was no difference in gap duration between the two treatments applied to defenders.

The mean duration of gaps again did not vary from bout to bout but in contrast to the early stage of each bout there were no significant interaction effects between bout number and any other factor. The duration of gaps did, however, continue to increase within bouts ( $F_{3,75} = 4.5, p < 0.001$ ). There were no further interaction effects.

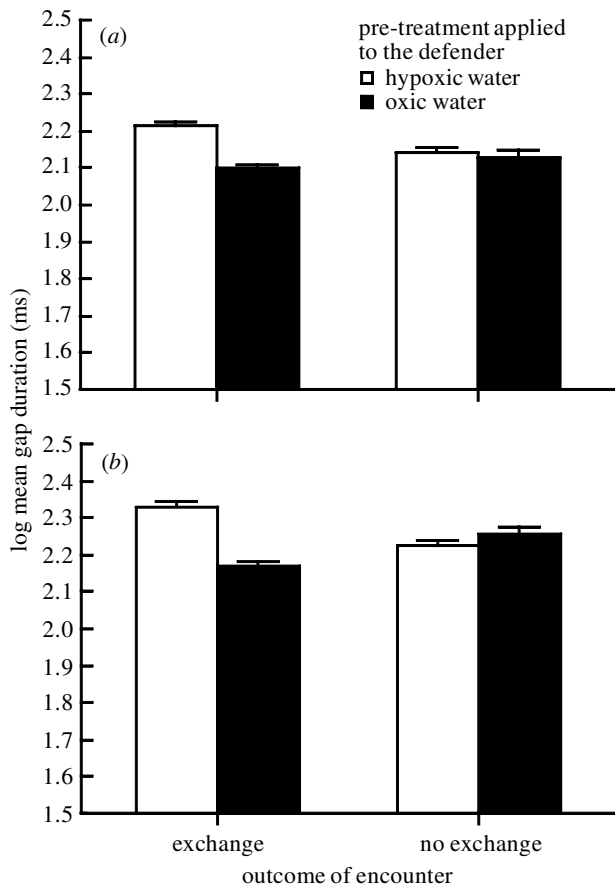


Figure 3. The interaction effect of the pre-treatment applied to defenders and the outcome of the encounter on the duration of (a) the first four gaps and (b) the last four gaps of the first six bouts of rapping. Error bars show s.e.

#### (c) Number of raps in each bout

Attackers that were pre-treated with oxic water performed more raps per bout during the first six bouts than did those pre-treated with hypoxic water ( $F_{1,53} = 13.2$ ,  $p < 0.001$ ). The number of raps was not affected by the pre-treatment applied to defenders or by the eventual outcome of the encounter. There was, however, a significant interaction effect between the pre-treatment of the attacker and the outcome of the encounter ( $F_{1,53} = 7.6$ ,  $p < 0.01$ ) (figure 5); hypoxic attackers that effected an exchange performed more raps per bout than those that did not exchange, but with oxic initiators the difference between the two outcomes was less marked.

The number of raps performed per bout decreased during bouts 1 to 6 ( $F_{5,269} = 13.2$ ,  $p < 0.001$ ). Comparisons of means show that bouts 1 ( $F_{1,290} = 18.8$ ,  $p < 0.0001$ ) and 2 ( $F_{1,290} = 11.0$ ,  $p < 0.001$ ) contained more raps than bout 3, but bout 3 contained less than bout 4 ( $F_{1,290} = 5.9$ ,  $p < 0.05$ ) (figure 6). There were no interaction effects between bout number and any other variables.

#### (d) Duration of pauses between bouts

Attackers that were pre-treated with oxic water left shorter pauses between bouts of rapping than did those treated with hypoxic water ( $F_{1,48} = 5.8$ ,  $p < 0.05$ ), the duration of pauses was also shorter when defenders were treated with hypoxic water prior to the encounters

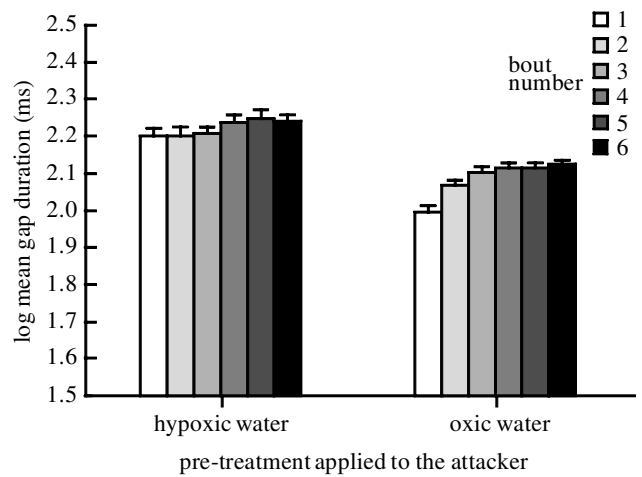


Figure 4. The interaction effect between bout number and the pre-treatment applied to attackers. Error bars show s.e.

( $F_{1,48} = 5.2$ ,  $p < 0.05$ ) and crabs that effected an exchange left shorter pauses than those that did not exchange ( $F_{1,48} = 7.4$ ,  $p < 0.01$ ). There was a two-factor interaction effect between the pre-treatment applied to the attacker and the outcome of encounters ( $F_{1,48} = 14.9$ ,  $p < 0.0005$ ) (figure 7); for crabs that effected an exchange those treated with oxic water had shorter pauses than those treated with hypoxic water but for those not effecting an exchange there was no difference. The duration of pauses did not vary from pause to pause and there were no interaction effects between pause number and any other factors.

#### (e) Duration of fights

The total number of raps and the total number of bouts performed by initiators were not affected by the treatment applied to attackers or defenders, by the outcome of the encounter or by the RWD between the two crabs. When crabs that did not evict the opponent were excluded from the analysis, however, there was a non-significant trend for hypoxic large crabs to perform fewer bouts than those exposed to oxygenated water ( $F_{1,47} = 3.3$ ,  $p < 0.1$ ).

### 4. DISCUSSION

Low oxygen prior to contests had marked effects on the behaviour of potential initiators of fights. They were less likely to initiate a fight than those that were treated with oxygenated water and those that did attack fought less vigorously. They left longer pauses between bouts of rapping, performed fewer raps in each bout, and these raps were separated by gaps of greater duration. These are clear indications that exposure to hypoxic conditions induces increased levels of fatigue. Furthermore, attackers treated with hypoxic water that rapped were less likely to evict the opponent. Treatment with hypoxic water did not, however, have similar effects on defenders; there was no difference in the likelihood of being evicted between hypoxic and oxic crabs.

Previous studies (Briffa *et al.* 1998; Briffa & Elwood 2000a,b) have clearly demonstrated a relationship between the vigour of rapping and the likelihood of the defender being evicted and indicate that defenders use the

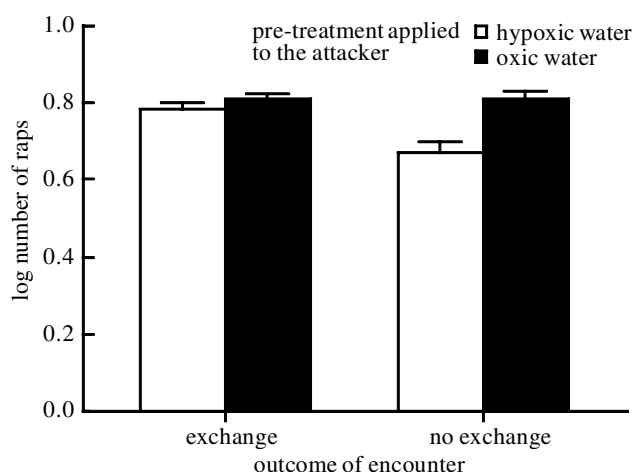


Figure 5. The interaction effect between the outcome of the encounter and the pre-treatment applied to attackers on the number of raps performed during the first six bouts of rapping. Error bars show s.e.

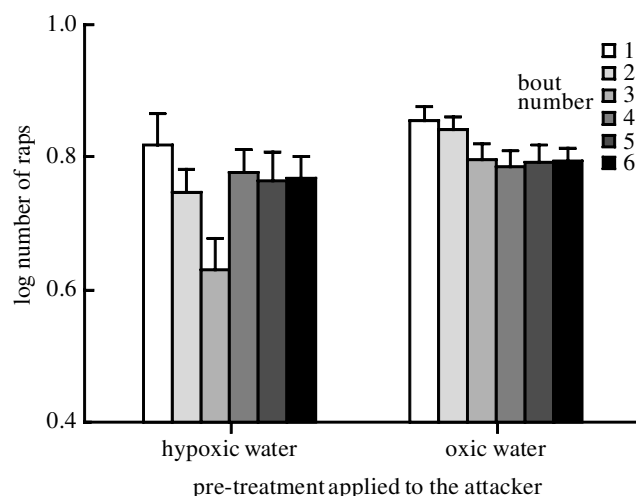


Figure 6. The effect of bout number on the number of raps performed in each of the first six bouts for attackers treated with hypoxic and oxygenated water. Errors bars show s.e.

pattern of rapping to assess the ability of the attacker. One possible reason for the difference between the effects of hypoxia on the two roles is that, in reaching the decision to release the shell, defenders compare the rate of rapping in attackers with an absolute threshold rate, rather than with a relative one. In the case of a relative threshold, hypoxic attackers, for example, would rap with reduced vigour but hypoxic defenders, equally affected by increased fatigue, would still be expected to release their shells since the signal of the attacker's ability, relative to that of defenders, would be the same as under oxic conditions. Similarly, attackers would be expected to evict hypoxic defenders more readily than defenders supplied with oxic water since any relative threshold would be crossed sooner. Thus we would expect to see hypoxic defenders being evicted more readily than those supplied with oxic water, but the data do not support this. If, however, defenders compared the vigour of rapping with an absolute threshold, hypoxic attackers would be less likely to attain the required vigour of rapping for effecting an eviction, regardless of the condition of defenders, because of the effects of fatigue. Thus, one would expect the pattern, shown by the data, of hypoxic attackers being less likely to effect an exchange than those supplied with oxic water, but no difference between the two groups of defenders.

This explanation assumes that the effects of hypoxia on the ability of attackers to rap are more immediate than any effects on the decision rule used by defenders. This is reasonable because attackers perform vigorous activity whereas defenders are tightly withdrawn into their shells and perform only occasional 'cheliped flicking', a low-intensity defensive activity. Thus, the only costs accrued by defenders are time-costs and those which might be incurred directly by being rapped. An alternative explanation for the lack of effect of hypoxia in defenders is that rapping acts solely on the basis of the direct detrimental effects that it might incur on defenders, and that these are independent of the level of fatigue in defenders. Various detrimental effects of rapping have been suggested (Elwood & Neil 1992; Briffa & Elwood 2000b) and it is difficult to see how rapping could act as a pure signal.

One possible detrimental effect is the disruption of respiration (Elwood & Neil 1992) but the present data do not support this. Other possibilities include disruption of the sensory organs causing disorientation (Elwood & Neil 1992) and reflex stiffening of the abdominal muscles (Briffa & Elwood 2000b). The variation in the temporal pattern of signalling described by Briffa *et al.* (1998), however, would not be expected if there was no signalling component of the activity and suggests that, in addition to incurring any detrimental effects, rapping also advertises information about the attacker.

Curiously, the pre-treatment applied to defenders affected the behaviour of attackers. Attackers appear to put less effort into rapping shells occupied by hypoxic defenders; large crabs that are treated with oxic water leave longer gaps when rapping a hypoxic defender than when rapping a defender treated with oxic water but hypoxic attackers leave relatively long gaps regardless of the condition of the defender (figure 2a,b). Furthermore, attackers that evicted hypoxic defenders left longer gaps than those evicting oxic defenders (figure 3a,b). These effects are unexpected and suggest that attackers are able to obtain more information about the opponent either prior to rapping, or perhaps during rapping by pulling at the chelipeds between bouts, than was previously thought. Interestingly, there is no difference in the number of raps that attackers must perform, in order to effect an eviction, between attackers that initiate fights with hypoxic and oxic defenders. Thus there appears to be a trade-off between contest duration and the vigour of fighting and the data suggest that it is less costly to engage in relatively long low-intensity fights than short vigorous fights. The time-costs of these fights must therefore increase sub-linearly such that a doubling of contest duration would result in a less than twofold increase in time associated costs. This is predicted by the energetic assessment model (Payne & Pagel 1997), which shows that if the intensity of signalling both increases and decreases during the course of an encounter (as is the case with shell fights; Briffa *et al.* 1998) costs of fighting must increase in this way.

The decrease in effort by attackers that rap hypoxic defenders means that any absolute threshold used by

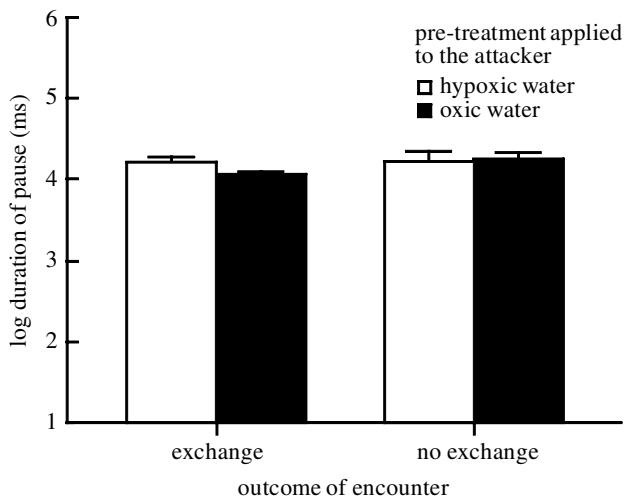


Figure 7. The interaction effect between the outcome of the encounter and the pre-treatment applied to attackers. Error bars show s.e.

defenders must be arrived at by a combination of the vigour of rapping and the duration of fights, such that the threshold could be crossed either by rapping vigorously for a relatively short period or by rapping less vigorously but over a longer period of time. The data also indicate that the decision rule used by defenders must be in some way altered by hypoxic treatment, perhaps because some detrimental effect of rapping is increased by fatigue. Any effect of hypoxia on the decision rule used by defenders, however, does not rule out the possibility that they use an absolute threshold in reaching their decision, as long as the effect on the attacker's ability to rap is more immediate. Any absolute threshold level of signalling, that defenders use as a decision rule, is not compatible with the sequential assessment game (Enquist & Leimar 1983; Enquist *et al.* 1990), since the ESS for this model is to use a relative threshold as a switching line. This provides further support for the previous studies which suggest that shell rapping provides a cumulative signal of attacker RHP. Another possible example of use of a relative threshold in determining the duration of agonistic behaviour is provided by the study by Bridge *et al.* (2000) of fighting in the orb-weaving spider *Metellina maugei*. Although they found a positive correlation between relative size difference and fight durations, as would be predicted by the sequential assessment model (Enquist & Leimar 1983) and earlier models (e.g. Maynard Smith 1982), stronger correlations were reported between contest duration and the actual size of losers. Thus, it appears that in this species also, giving up time might be determined by the use of an absolute threshold.

The increase in gap duration that occurs as the fight progresses, reported here and previously (Briffa & Elwood 2000a), indicates that rapping induces fatigue and that the rate of rapping is therefore determined by the stamina (i.e. resistance to fatigue) of the attacker. In oxic crabs the duration of gaps starts relatively low but increases rapidly, whereas in hypoxic attackers the initial duration is much higher but there is only a slight increase in duration from bout to bout (figure 4). Thus, although the initial vigour of rapping (i.e. the inverse of gap

duration) is greater in attackers supplied with oxic water the effects of fatigue become apparent more quickly. There are two possible explanations for this. First, the pattern of increasing gap durations, seen in oxic and hypoxic attackers, could represent early and late phases of the same fatigue curve. The pattern of increase seen in oxic crabs represents the early stage of the contest where fatigue levels start low but increase rapidly, causing a decrease in the rate of activity. The pattern shown by hypoxic attackers would then be analogous to that expected during the later stages of normal (i.e. oxic) fights where the rate of activity reaches a plateau, although fatigue levels might be expected to continue to increase. This is compatible with the idea that defenders compare the vigour of rapping with an absolute threshold, such that this plateau would represent the minimum level of signalling required to effect an eviction.

An alternative explanation relates to the cumulative assessment model (Payne 1998) in which the contestant's decision rule is based on the sum of the opponent's performances. This model predicts that losers, or contestants that are likely to lose because they are of poorer quality or in poorer condition, should initially signal at a level below that of winners but escalate the level more quickly. From this it follows that any de-escalation in the rate of signalling, particularly if de-escalation occurs in both good and relatively poor quality attackers, should occur more slowly in poor quality contestants than in the good quality contestants, as is seen in the present data.

These two possible explanations for the difference in the pattern of change in gap duration between the two groups of attackers cannot be distinguished by the present data. If the gap durations of entire fights, staged under normal conditions, were examined, however, an increase in the duration of gaps at a consistent rate would discount the first possibility, whereas the appearance of a plateau, particularly during the first half of fights, would tend to rule out the second possibility. This would also be true for any analysis of the temporal pattern of signalling in other animals that settle contests by the use of repeated displays. In this way the prediction of the cumulative assessment model (Payne 1998), that losers should escalate the level of signalling faster than winners, could be further tested. The only other animal reported to show behaviour compatible with this prediction of the model is the cyprinodont fish *Aphyosemion striatum* (Dow *et al.* 1976; Payne 1998). The model appears particularly suited to the case of shell fighting in hermit crabs because (i) it can be applied to both dangerous and non-dangerous displays, as long as the display incurs some cost to the signaller, and (ii) because it requires no matching of signalling levels between winners and losers. This stipulation of the energetic war of attrition (Payne & Pagel 1997), highlighted by Payne (1998), is difficult to apply to the case of shell fighting in hermit crabs since the two crabs perform different activities, although it could be assumed that attackers attempt to 'match' the threshold level of signalling that defenders use for their decision rule.

The ability to manipulate receivers and signallers independently greatly helps resolution of the assessment and decision rules underlying agonistic encounters between animals. By manipulating the level of oxygen in the water

separately for attackers and defenders it has been possible to examine how stamina determines the behaviour of the two roles. These data confirm the suggestion of Briffa & Elwood (2000a) that the temporal pattern of shell rapping is mediated by fatigue and could advertise the stamina of attackers. Furthermore, it appears that attackers give up when the effects of fatigue prevent them from rapping effectively. Shell rapping is unlikely to be a pure signal but it appears that any disruption to the defender's ability to respire effectively is minimal. Thus, the decision of defenders to give up does not appear to be related to fatigue and the exact nature of any detrimental effects of shell rapping remain unclear. The data show that rapping could act as a cumulative signal of attacker stamina, but are not congruent with the sequential assessment model. The negotiation model of shell exchange makes no predictions about variation in the pattern of rapping and previous analyses of this uphold the view that shell fights are aggressive interactions (Briffa *et al.* 1998; Briffa & Elwood 2000a,b). Similarly, the negotiation model makes no assumption that the rate of rapping should be dependent on the ability or condition of the attacker. The present data, therefore, also support the aggression model of shell exchange.

We thank the UK Biotechnology and Biological Sciences Research Council for funding this work and an anonymous referee whose constructive comments have helped us to make considerable improvements to the manuscript.

## REFERENCES

- Bridge, A. P., Elwood, R. W. & Dick, J. T. A. 2000 Imperfect assessment and limited information preclude optimal strategies in male–male fights in the orb-weaving spider *Metellina mengei*. *Proc. R. Soc. Lond. B* **267**, 273–279.
- Briffa, M. & Elwood, R. W. 2000a Analysis of the fine scale timing of repeated signals: does shell rapping in hermit crabs signal stamina? *Anim. Behav.* **59**, 159–165.
- Briffa, M. & Elwood, R. W. 2000b The power of shell rapping influences rates of eviction in hermit crabs. *Behav. Ecol.* **11**, 288–293.
- Briffa, M., Elwood, R. W. & Dick, J. T. A. 1998 Analysis of repeated signals during shell fights in the hermit crab *Pagurus bernhardus*. *Proc. R. Soc. Lond. B* **265**, 1467–1474.
- Clutton Brock, T. H. & Albon, S. D. 1979 The roaring of red deer and the evolution of honest advertisement. *Behaviour* **69**, 145–170.
- Clutton-Brock, T. H., Albon, S. D., Gibson, R. M. & Guinness, F. E. 1979 The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus* L.). *Anim. Behav.* **27**, 211–225.
- Côté, I. M., Bénédict, R. & Cooke, P. K. 1998 Less choosy or different preference? Impact of hypoxia on hermit crab shell assessment and selection. *Anim. Behav.* **56**, 867–873.
- Dow, M., Ewing, A. W. & Sutherland, I. 1976 Studies on the behaviour of cyprinodont fish. III. The temporal patterning of aggression in *Aphyosemion striatum* (Boulenger). *Behaviour* **59**, 252–268.
- Dowds, B. M. & Elwood, R. W. 1983 Shell wars: assessment strategies and the timing of decisions in hermit crab shell fights. *Behaviour* **85**, 1–24.
- Dowds, B. M. & Elwood, R. W. 1985 Shell wars. II. The influence of relative size on decisions made during shell fights. *Anim. Behav.* **29**, 1239–1244.
- Elwood, R. W. & Glass, C. W. 1981 Negotiation of aggression during shell fights of the hermit crab *Pagurus bernhardus*? *Anim. Behav.* **29**, 1239–1244.
- Elwood, R. W. & Neil, S. J. 1992 *Assessments and decisions: a study of information gathering by hermit crabs*. London: Chapman & Hall.
- Elwood, R. W., Wood, K. E., Gallagher, M. B. & Dick, J. T. A. 1998 Probing motivational state during agonistic encounters in animals. *Nature* **393**, 66–68.
- Enquist, M. & Leimar, O. 1983 Evolution of fighting behaviour: decision rules and assessment of relative strength. *J. Theor. Biol.* **102**, 387–410.
- Enquist, M. & Leimar, O. 1987 Evolution of fighting behaviour: the effect of variation in resource value. *J. Theor. Biol.* **127**, 187–205.
- Enquist, M., Leimar, O., Ljunberg, T., Mallner, Y. & Segerdahl, N. 1990 A test of the sequential assessment game: fighting in the cichlid fish *Nannacara anomala*. *Anim. Behav.* **40**, 1–14.
- Hazlett, B. A. 1978 Shell exchanges in hermit crabs: aggression, negotiation, or both? *Anim. Behav.* **26**, 1278–1279.
- Hazlett, B. A. 1983 Interspecific negotiations: mutual gain in exchanges of a limiting resource. *Anim. Behav.* **31**, 160–163.
- Hazlett, B. A. 1987 Information transfer during shell exchange in the hermit crab *Calcinus tibicen*. *Anim. Behav.* **35**, 218–226.
- Hazlett, B. A. 1996 Assessments during shell exchanges by the hermit crab *Clibanarius vittatus*, the complete negotiator. *Anim. Behav.* **51**, 567–573.
- Jackson, N. W. 1988 Information gathering and decision making during shell selection by the hermit crab *Pagurus bernhardus*. PhD thesis, The Queen's University of Belfast, UK.
- Lambrechts, M. M. & Dhondt, A. A. 1988 The anti-exhaustion hypothesis: a new hypothesis to explain song performance and song switching in the great tit. *Anim. Behav.* **36**, 327–334.
- Maynard Smith, J. 1982 *Evolution and the theory of games*. Cambridge University Press.
- Payne, R. J. H. 1998 Gradually escalating fights and displays: the cumulative assessment model. *Anim. Behav.* **56**, 651–662.
- Payne, R. J. H. & Pagel, M. 1996 Escalation and time costs in displays of endurance. *J. Theor. Biol.* **183**, 185–193.
- Payne, R. J. H. & Pagel, M. 1997 Why do animals repeat displays? *Anim. Behav.* **54**, 109–119.
- Smith, I. P. & Taylor, A. C. 1993 The energetic cost of agonistic behaviour in the velvet swimming crab, *Necora (= Liocarcinus) puber* (L.). *Anim. Behav.* **45**, 375–391.
- Thorpe, K. E., Taylor, A. C. & Huntingford, F. A. 1995 How costly is fighting? Physiological effects of sustained exercise and fighting in swimming crabs, *Necora puber* (L.) (Brachyura, Portunidae). *Anim. Behav.* **50**, 1657–1666.
- Weary, D. M., Lambrechts, M. M. & Krebs, J. R. 1991 Does singing exhaust male great tits? *Anim. Behav.* **41**, 540–542.

As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.